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Abstract: Bioenergy is a major component of the global transition to renewable energy technologies. The plant and fungal kingdoms offer great potential but remain mostly untapped. Their increased use could contribute to the renewable energy transition and addressing the United Nations Sustainable Development Goal 7 “Ensure access to affordable, reliable, sustainable and modern energy for all.” Current research focuses on species cultivated at scale in temperate regions, overlooking the wealth of potential new sources of small-scale energy where they are most urgently needed. A shift towards diversified, accessible bioenergy technologies will help to mitigate and adapt to the threats of climate change, decrease energy poverty, improve human health by reducing indoor pollution, increase energy resilience of communities, and decrease greenhouse gas emissions from fossil fuels.

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REVIEW

Plant Power: Opportunities and challenges for meeting sustainable energy needs from the plant and fungal kingdoms

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Societal Impact Statement

Bioenergy is a major component of the global transition to renewable energy technologies. The plant and fungal kingdoms offer great potential but remain mostly untapped. Their increased use could contribute to the renewable energy transition and addressing the United Nations Sustainable Development Goal 7 “Ensure access to affordable, reliable, sustainable and modern energy for all.” Current research focuses on species cultivated at scale in temperate regions, overlooking the wealth of potential new sources of small-scale energy where they are most urgently needed. A shift towards diversified, accessible bioenergy technologies will help to mitigate and adapt to the threats of climate change, decrease energy poverty, improve human health by reducing indoor pollution, increase energy resilience of communities, and decrease greenhouse gas emissions from fossil fuels.

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Summary

Bioenergy derived from plants and fungi is a major component of the global transition to renewable energy technologies. There is rich untapped diversity in the plant and fungal kingdoms that offers potential to contribute to the shift away from fossil fuels and to address the United Nations Sustainable Development Goal 7 (SDG7) “Ensure access to affordable, reliable, sustainable and modern energy for all.” Energy poverty—the lack of access to modern energy services—is most acute in the Global South where biodiversity is greatest and least investigated. Our systematic review of the literature over the last 5 years (2015–2020) indicates that research efforts have targeted a very small number of plant species cultivated at scale, mostly in temperate regions. The wealth of potential new sources of bioenergy in biodiverse regions, where the implementation of SDG7 is most urgently needed, has been largely overlooked. We recommend next steps for bioenergy stakeholders—research, industry, and government—to seize opportunities for innovation to alleviate energy poverty while protecting biodiversity. Small-scale energy production using native plant species in bioenergy landscapes overcomes many pitfalls associated with bioenergy crop monocultures, such as biodiversity loss and conflict with food production. Targeted trait-based screening of plant species and biological screening of fungi are required to characterize the potential of this resource. The benefits of diversified, accessible bioenergy go beyond the immediate urgency of energy poverty as more diverse agricultural landscapes are more resilient, store more carbon, and could also reduce the drivers of the climate and environmental emergencies.

KEYWORDS

Bioenergy, biofuel, biogas, energy poverty, feedstock, renewables, research effort, sustainable energy

1 | THE PLANT AND FUNGAL KINGDOMS AS A SOURCE OF ENERGY

Almost every aspect of contemporary human activity depends on the availability of energy. Nevertheless, in 2017 an estimated 840 million people, mostly in sub-Saharan Africa, Asia, and Oceania (excluding Australia and New Zealand) did not have access to electricity (United Nations, 2019). Furthermore, c. 3 billion people lack clean cooking fuels and technologies, and cook using inefficient and polluting technologies fuelled by firewood or kerosene (United Nations, 2019) (Figure 1). One of the United Nations Sustainable Development Goals, SDG 7, aims to address energy poverty—a lack of access to electricity and energy for cooking—by “ensuring access to affordable, reliable, sustainable and clean energy for all” by 2030 (United Nations, 2015). This will require balancing the energy “trilemma”: energy security, energy equity (accessibility and affordability), and environmental sustainability to deliver healthy energy systems (World Energy Council, 2019). Progress towards SDG 7 needs a range of solutions appropriate for different environments, scales, and cultures. Bioenergy derived from plants, fungi, and algae has potential to play an important

role in alleviating energy poverty while supporting and protecting biodiversity. However, targeted research is needed to facilitate the implementation of biodiverse production systems, modern technologies, and improved environmental and economic indicators based on robust scientific evidence.

Bioenergy is derived from natural resources—predominantly plants and fungi—for generating electricity, cooking, transportation fuel, and domestic heating and cooling (Box 1). Within the last 10–20 years, biofuels and renewable energy sources such as geothermal resources, wind, and solar, have helped to diversify the global energy economy and reduce carbon emissions (IEA, 2019). Replacing fossil fuels with clean bioenergy significantly reduces air pollution and greenhouse gas emissions (Qin et al., 2015, 2018). The plant and fungal kingdoms, *Plantae* and *Fungi*, respectively, are distantly related (fungi are more closely related to the animal kingdom, *Animalia* than plants) but ecologically linked as plants depend on endophytic fungi and root mycorrhizae for their very existence (an estimated 90% of plant species have root-based mycorrhizae) and to enhance nutrition, defense, and reproduction (Willis, 2018). The plant kingdom is relatively well understood with ca. 350,000 species (WCVP, 2020) and ca. 10%–20% of “known unknown” species yet to

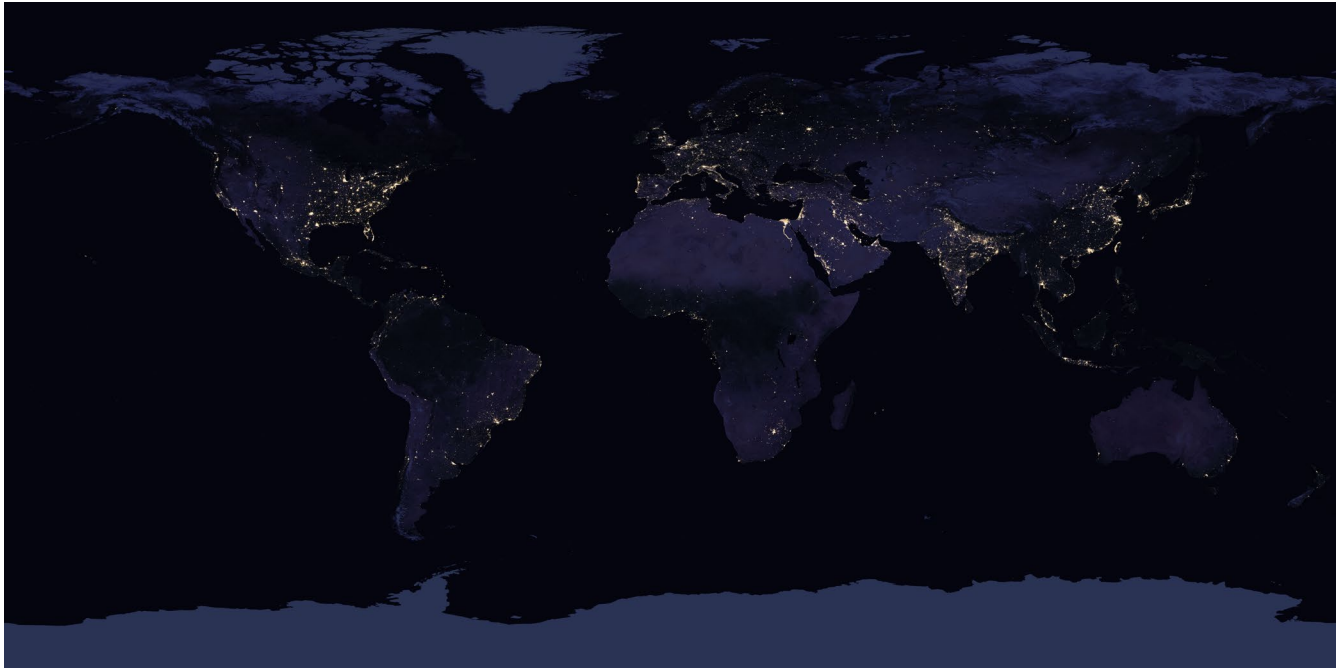


FIGURE 1 The iconic NASA “Earth at Night” 2016 satellite image provides a compelling illustration of energy poverty (<https://earthobservatory.nasa.gov/features/NightLights/page3.php>). Approximately 11% of the global population, mostly in the Global South, do not have access to electricity, which includes 56% in sub-Saharan Africa, 37% in Oceania (excluding Australia and New Zealand), 9% in Central and Southern Asia, 5% in Northern Africa and Western Asia, 2% in Eastern and South-Eastern Asia, Latin America and the Caribbean, while the populations of Europe and North America all have access to electricity (United Nations, 2019)

be scientifically documented (Joppa, Roberts, Myers, & Pimm, 2011). In contrast, only 148,000 species of fungi are named and classified (Species Fungorum, 2020) from an estimated 2.2–3.8 million species (Hawksworth & Lücking, 2017). Proportionally, the number of fungal species being used to generate or enhance bioenergy processing would appear to be minimal compared to the plant kingdom which yields primary and derived bioenergy (Box 1) and basic biodiversity research is needed to enable better utilization.

At least 2,500 plant species are documented sources of fuel or bioenergy, representing 1,090 genera and 188 families according to the World Checklist of Selected Plant Families (Box 2). This diversity appears to follow global patterns in plant diversity and economic development (Kier et al., 2009) with the highest diversity of native fuel species in biodiverse regions of the Global South, and highest numbers of introduced (non-native) species used in the northern hemisphere (Figure 2). In the quest for renewable energy sources to replace fossil fuels, a very narrow sampling of the pool of 350,000 species (<https://wcvp.science.kew.org>) in the plant kingdom has become the principal source of bioenergy (Figure 3). Just three species in the grass family Poaceae yield 89% of global industrial bioethanol: maize, *Zea mays* L., sugarcane, *Saccharum officinarum* L. and wheat, *Triticum aestivum* L. (OECD & FAO, 2019). Biodiesel is derived mostly from soybean (*Glycine max* L. Fabaceae), palm oil (primarily *Elaeis guineensis*, Arecaceae), and rapeseed oil (*Brassica napus* L., Brassicaceae) and these “staple” bioenergy plants are also important food crops. More than half the global plant-based energy consumed by humans is provided by four species in the grass family, Poaceae: sugarcane, wheat, rice (*Oryza sativa* L.), and maize (OECD & FAO,

2019). “Food versus fuel” conflicts have arisen because technical solutions for deriving bioenergy from plants have been developed for industrial agriculture monocultures, with its very narrow biodiversity base.

Bioenergy has also been implicated in land access issues, habitat transformation, and biodiversity loss (Blanchard, O’Farrell, & Richardson, 2015; Bonsch, Humpenöder, Popp, & Bodirsky, 2016; Lovett, Hards, Clancy, & Snell, 2011; Luque et al., 2010; Poudyal & Lovett, 2010; Santangeli et al., 2016) which, in turn, contribute to the climate emergency (Creutzig et al., 2015; Gills & Morgan, 2019). Rising global demand for palm oil for food and biofuels had stimulated the conversion of 2.3 million ha of peat swamp forest for oil palm plantations by 2010 on the Malay Peninsula, Borneo, and Sumatra (Koh, Miettinen, Liew, & Ghazoul, 2011). Biofuel crop plantations are likewise implicated of deforestation in the Amazon in South America, despite cattle farming and soy cultivated for animal feed accounting for over 80% of pasture expansion in the period 2005–2013 (Barona, Ramankutty, Hyman, & Coomes, 2010; da Costa, Matricardi, Pedlowski, Cochrane, & Fernandes, 2017; Gollnow, Hissa, Rufin, & Lakes, 2018; Pendrill, Persson, Godar, & Kastner, 2019). Modeling simulations with an increased global ethanol demand by 2030 predict sugarcane driving expansion of agriculture into the natural vegetation of the Cerrado and Amazon (van der Hilst, Verstegen, Woltjer, Smeets, & Faaij, 2018). In the short term, the direct impact of biofuel production on deforestation in the Amazon will likely be amplified following the lifting in 2019 of a ban on sugarcane cultivation in the Amazon, to boost biofuel production (Ferrante & Fearnside, 2020). Wood fuel harvesting is a

Box 1 What is plant power?

Through photosynthesis, plants possess the remarkable ability to locally reduce entropy by capturing solar energy to build complex molecules from simple ones. Humans release this bioenergy using a range of technologies, the simplest of which is igniting fuel between the stones of a hearth to provide energy for cooking and warmth. Archaeological evidence suggests that the controlled use of fire has been used for at least 350–400 thousand years by several *Homo* species (*H. erectus*, *H. neanderthalensis*, *H. sapiens*) (MacDonald, 2017; Sandgathe & Berna, 2017). Modern technologies to release “plant power” fall broadly into two categories: thermal and biological, and each requires different feedstock.

Primary biofuels. Wood and charcoal generate an estimated 9% of primary bioenergy (derived directly from the plant material) for three billion people, mostly in the Global South (Bailis et al., 2015; United Nations, 2015). Smoke from open fires, known as the “killer in the kitchen” has significant health implications that disproportionately affect women and children (Gordon et al., 2014; Olopade et al., 2017; Perez-Padilla, Schilman, & Riojas-Rodriguez, 2010; Smith et al., 2011; Thorsson et al., 2014). Clean energy technologies and fuels such as small-scale anaerobic digesters for biogas production and improved cooking stoves using sustainably harvested wood, biochar, bio-briquettes, and pellets are in development (Champion & Grieshop, 2019; Dinesha, Kumar, & Rosen, 2019; Garfí, Martí-Herrero, Garwood, & Ferrer, 2016; Gitau, Mutune, Sundberg, Mendum, & Njenga, 2019; Johnson et al., 2019; Orskov, Yongabi Anchang, Subedi, & Smith, 2014; Rajendran, Aslanzadeh, & Taherzadeh, 2012; Vasco-Correa, Khanal, Manandhar, & Shah, 2018) (cleancookingalliance.org). In the northern hemisphere, lignocellulosic biomass such as white wood pellets produced from forestry residues and solid fuels such as *Miscanthus* (Poaceae) and *Salix* (Salicaceae) are used in thermal power plants. Besides primary energy and electricity, biomass can also produce heat and transport fuels, as well as bio-based materials and biochemicals.

Liquid biofuels. Bioethanol accounts for two-thirds of liquid biofuels used in the transportation sector globally (OECD and FAO, 2019). It is derived from fermented high sugar crops (beets, *Beta vulgaris* L., Amaranthaceae; sugarcane, *Saccharum officinarum* L., Poaceae) and starchy crops (wheat; maize, *Zea mays*, both Poaceae). An array of cellulose-rich biomass feedstocks (corn stover; switchgrass, *Panicum virgatum* L., Poaceae; *Miscanthus*; wood chips) are used in second generation technologies which generate biofuels using fermentation or thermal processes. For biodiesel production, plants containing high yields of extractable lipids are required and the suitability of the feedstock is contingent on the fatty acid chain length and saturation of the lipids (Demirbas, 2010; Pinzi, Mata-Granados, Lopez-Gimenez, Luque de Castro, & Dorado, 2011; Wahyudi, Widodo, & Wijayanti, 2018). Oil content is therefore not necessarily a direct indication of biodiesel suitability. The main sources of biodiesel are vegetable oils (soybean, *Glycine max* (L.) Merr., Leguminosae; palm, *Elaeis*, Arecaceae; and rapeseed, *Brassica napus* Vilm., Brassicaceae) and waste cooking oils (OECD & FAO, 2019).

Emerging sources. A significant new supply chain based on wet feedstocks such as invasive aquatic plants (e.g. water hyacinth, *Pontederia crassipes* (= *Eichhornia crassipes*, Pontederiaceae) is emerging in the Global South; plant material cleared from large water bodies that would usually be left to decompose can instead be processed to yield thermal energy, electricity, and bioethanol (Patel, 2012; Santibañez-Aguilar, Ponce-Ortega, González-Campos, Serna-González, & El-Halwagi, 2013; Varanasi, Kumari, & Das, 2018). In dry environments, fast-growing succulent plant species suitable for cultivation on marginal soils with limited irrigation hold promise as bioenergy feedstocks (Yang, Lu, et al., 2015; Yang, Cushman, et al., 2015). Also as succulence, plants that utilize the crassulacean acid metabolism photosynthesis pathway exhibit improved heat/drought durability and water-use efficiency. Genera such as *Agave* spp. (Asparagaceae) and *Opuntia* spp. (Cactaceae) have been highlighted for their potential as bioenergy feedstocks in drylands that far exceeds current production levels (Davis, Kuzmick, Niechayev, & Hunsaker, 2017; Davis et al., 2014, 2019; Mason et al., 2015). Plants with enhanced heat/ drought resistance will help to reduce global production requirements of *Triticum* spp. (wheat) and *Zea mays* (maize), both used for bioenergy feedstocks, which have already been linked to climate change (Field, Barros, Dokken, & Mach, 2014; Lobell, Schlenker, & Costa-Roberts, 2011). High carbohydrate content feedstocks are favored for fermentation, although pre-treatment is necessary to hydrolyze structural carbohydrates into fermentable sugars. Anaerobic digestion yields biogas (a mixture of methane and carbon dioxide) from feedstocks containing high carbohydrate, fat, and protein content such as agricultural and municipal waste, animal and human wastes. Anaerobic digestion is widely used in Asia, notably China and India, where millions of small-scale community anaerobic digester systems are in operation (Ahammad & Sreekrishnan, 2016), and it has potential in Africa to replace wood and charcoal cooking fuels. However, significant cultural and socio-economic barriers to household adoption of biogas technology persist, from awareness to installation of digesters, training and market opportunities (Clemens, Bailis, Nyambane, & Ndung'u, 2018; Rupf, Bahri, de Boer, & McHenry, 2015). In the northern hemisphere, anaerobic digestion has been implemented at large scales for treatment of sludge, food waste, and agricultural waste, generating combined heat and power or upgraded to produce bio-methane for the gas grid or transport.

Box 1 (Continued)

A similar situation affects the development of new bioenergy sources derived from the algae kingdom. Micro- and macroalgae produce “third generation” biofuels, including renewable aviation fuel, bio-coal, and biogas, and are also used to capture, remove or transform pollutants such as excess nutrients and heavy metals from wastewater, and CO₂ from exhaust gases. Algae grow faster than terrestrial crops, but economic viability remains a challenge due to high processing costs preventing the wide-scale implementation of third generation energy solutions including algae, and advanced and lignocellulosic feedstocks (EPA, 2020). And yet, the species diversity and technological advances make algae a likely resource (Guarnieri & Pienkos, 2015; Guiry, 2012), like fungi, to yield major breakthroughs for sustainable bioenergy supplies in the future.

Box 2 Assessing the diversity of plant power

We assessed the diversity of energy plants and research efforts within the last 5 years to characterize their potential and possible drawbacks. We identified 2,582 species representing 1,909 genera in 188 plant families used for “fuel” from plant use records in the literature, standardized according to the Economic Botany Data Standard (Cook, 1995), and maintained in a database at the Royal Botanic Gardens, Kew, using the World Checklist of Vascular Plants taxonomy (Diazgranados et al., 2020; WCV, 2020). This resource is comprehensive but not exhaustive, as many fuel plants likely remain under-documented, notably in the tropics (Cámara-Leret & Dennehy, 2019). To accommodate incompleteness and possible geographical biases, known fuel species, including both native and introduced species, were mapped at Level 3 of the World Geographical Scheme for Recording Plant Distributions (WGSRPD) (Brummitt, 2001) (Figure 2a). The phylogenetic distribution of known fuel species was visualized (Figure 3) on a recent phylogeny of seed plants produced from DNA sequence data retrieved from the National Center for Biotechnology Information (NCBI) repository (Smith & Brown, 2018) comprising 449 plant families. The proportion of fuel species per family was optimized on the phylogeny using the *contMap* function in the R package PHYTOOLS (Revell, 2012).

We further explored regional geographical patterns in the diversity of fuel plant species by evaluating the list of fuel taxa against the World Checklist of Vascular Plants (WCV, 2020) (Figure 2b). Because fuel species richness is largely related to overall plant diversity and the area of a region, we also measured the proportion of fuel plant species per WGSRPD Level 3 region compared to the total number of vascular plant species [(number of fuel species)/(total number of vascular plant species)]. Lastly, we compared the geographic distribution of introduced fuel species versus all fuel species to detect patterns in the origins of fuel species. We found that a higher diversity of native fuel species, and fewer introduced species, are used in regions with greater plant diversity, such as sub-Saharan Africa (Figure 2c). Introduced fuel species are, overall, more common in the northern hemisphere.

We applied a systematic review approach to evaluate current research (2015–2020) on the plant and fungal kingdoms as sources of bioenergy. We defined three questions: “How are fungi enhancing bioenergy recovery from plants?”, “What are the risks and benefits of using plants for energy?”, and “How are new sources of energy from plants identified?” For each question, keyword searches (Methods S1) were carried out in English in two bibliographic databases (Scopus, <http://scopus.com/> and Web of Science, <http://webofknowledge.com/>). References were screened by title and abstract (Figure 4a). The results (Table S1) showed that research into plants and fungi for bioenergy spans plant science, agricultural, environmental and energy science, yet research efforts across these disciplines focus narrowly on bioenergy species already in use (Figure 4c), and on temperate crops (Figure 4b). Hence, research efforts within the past 5 years have overlooked the biodiversity-rich regions where energy poverty is most acute and where there is arguably the greatest potential for emerging technologies to use plants and fungi, including species whose energy potential have not yet been unlocked (Antonelli, Smith, & Simmonds, 2019).

major threat to forests in some areas, and has been exaggerated by land-use change leading to wood fuel scarcity. In wood fuel depletion hotspots (Bailis, Drigo, Ghilardi, & Masera, 2015) such as Nepal and Uganda, unsustainable forest harvesting supports 82%–90% of energy used, respectively, yet the majority of the population in both countries experience energy poverty (Baral et al., 2019; Jagger & Kittner, 2017; Mfitumukiza, Nambasa, & Walakira, 2019).

Traditional wood fuels account for 1.9%–2.3% (1.0–1.2 Gt CO₂e yr⁻¹) of global CO₂ emissions (Bailis et al., 2015) (and see Box 2). Unsustainable wood fuel harvesting is even more prevalent in the Earth's drylands, where water scarcity constrains the prevalence of trees in the landscape. Drylands occupy ca. 41% of global land area (Mortimore, 2009) and overlap with regions affected by energy poverty, particularly in Africa (United Nations, 2019). For example,

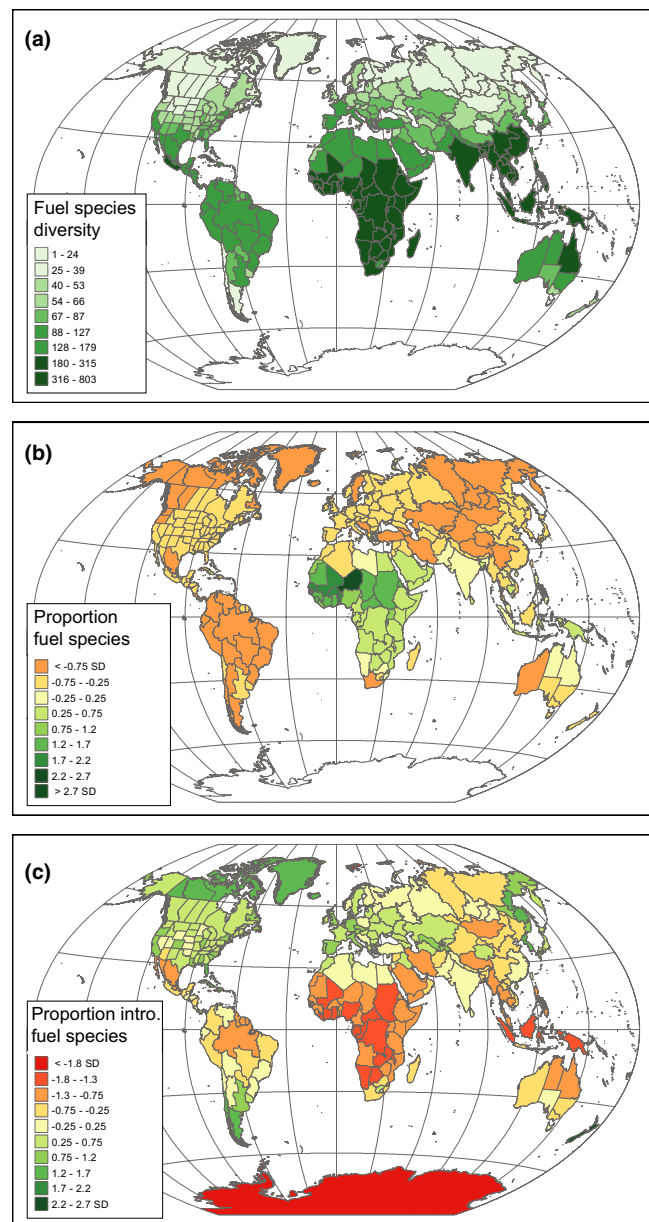


FIGURE 2 Global patterns in diversity and species richness of fuel plants recorded from the literature (see Box 2) showing (a) native and introduced fuel species (gradient legend using quantiles); (b) proportion of fuel species versus total species richness, standard deviation map with diverging palette; and (c) proportion of introduced (non-native) fuel species versus all fuel species, standard deviation map with diverging palette (for methods, see Box 2)

in the dryland areas of eastern Uganda, 98.8% of households use fuelwood for cooking and preserving food, mostly from *Acacia* spp. (Fabaceae) (Egeru, 2014). Simple measures such as incentives to grow preferred indigenous woody plants in small-holder agriculture and livestock systems, together with fuel-efficient cookstoves (Jetter & Kariher, 2009; Kees & Fieldmann, 2011) could significantly reduce loss of woodland cover.

Bioenergy landscapes have the potential to foster synergies between biodiversity, food, and energy production (Werling et al.,

2014). One promising concept is the community-based “energy garden,” pioneered by the Hassan Biofuels Park in southern India which gave rise to significant changes in national and state biofuel policy and legislation (Gowda, Prasanna, Kumar, & Haleshi, 2014). This approach identifies sustainable plant materials within the community and matches them to technologies supplying local bio-energy. It combines the cultivation of predominantly indigenous fuel plants on marginal or degraded land with the management of community forests, clearing invasive species, and use of agricultural and household waste to supply biomass for accessible energy processing technologies. Besides energy security, the system protects biodiversity, and improves food security (through agricultural productivity and ecosystem services such as pollinator provision) and water management (through erosion control) (Pariyar et al., 2016). The energy garden concept has been transferred to rural communities in Nepal (Pariyar et al., 2016). However, in order to ultimately displace fossil fuel combustion and reach net zero carbon emissions globally, some bioenergy solutions must also be scalable. Agroecosystem modeling in France, for instance, emphasized local factors such as soil type, meteorological data, and previous land-use largely impacting crop performance, and determined that using three biomass sources would use <3% of regional agricultural land and reduce greenhouse gas emissions by 60% (Dufossé, Drouet, & Gabrielle, 2016).

This review assesses the current role of the plant and fungal kingdoms in energy security and the potential for these natural resources to be developed in response to SDG 7 (United Nations, 2015). We focus on opportunities for local-scale interventions most relevant to addressing energy poverty at the community level. We summarize sources of bioenergy and associated technologies for deriving bio-energy from plants (Box 1) and fungi. Research trends are evaluated in a systematic literature review of plant-derived bioenergy (Box 2), as well as the lessons to be learned and approaches to accelerate development of new feedstocks for the future. Lastly, we recommend priorities for research and development that will help to harness the potential of the plant and fungal kingdoms for alleviating energy poverty while protecting and benefitting biodiversity and the ecosystem services they provide.

2 | CHALLENGES AND RISKS OF GETTING FROM PLANT TO POWER

Plants support the Earth's biosphere and occupy a unique position in the nexus of food, water, and energy resources. The cultivation or wild harvesting of fuel plants and the processing of plant waste as bioenergy feedstocks provides a cascade of environmental benefits for biodiversity, agricultural diversity, ecosystem services and water management, as well as the socio-economic benefits of energy security (Gu & Wylie, 2016; Sato, Intabon, & Maekawa, 2015; Stoms, Davis, Jenner, Nogueira, & Kaffka, 2012; Werling et al., 2014). Diversified landscapes and agroecological practices can mitigate the potentially negative downstream impacts of industrial bioenergy

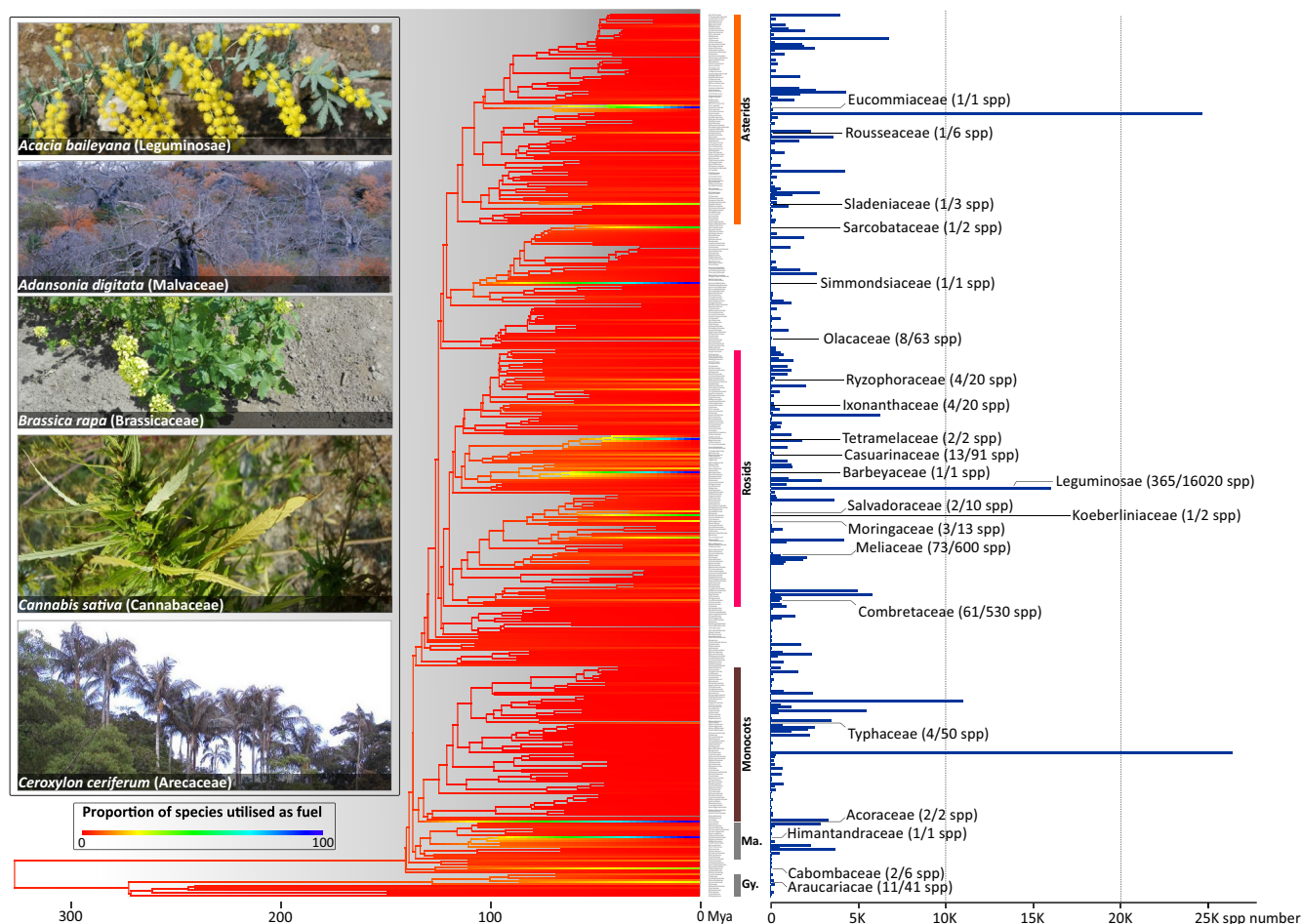


FIGURE 3 Global diversity of fuel plants recorded from the literature (see Box 2) expressed as the proportion of species per family on the tree of life for seed plants

supply chains (Holm-Nielsen & Ehimen, 2016; Yazan, Clancy, & Lovett, 2012), including the risks of commercial monoculture, including biodiversity loss, invasiveness, and susceptibility to commodity price fluctuations and political change.

The emergence of flex crops, cultivated for multiple purposes, have helped to reduce food versus fuel tensions in the bioenergy sector, but have been implicated in “land-grabbing” and major changes in land use, as investment funds move globally seeking high returns from commodities (Borras, Franco, Isakson, Levidow, & Vervest, 2016). The demand for flex crops is driven by major consumer and processing regions such as Europe, which are unlikely to meet their own regional demand for non-food crops, and rely heavily on imports from other world regions (two-thirds of the cropland required to meet the EU’s non-food biomass consumption is in other regions, mostly in China, the US, and Indonesia). The land-use impacts will require targeted policy making to avoid negative consequences being passed to low-income nations (Bruckner et al., 2019). Such impacts have been exemplified by a reduction in the European demand for palm oil in response to policy change governing sustainable biofuels in Europe that had a marked impact on the Indonesian supply chain, although these have not curtailed its environmental impact (Hinkes, 2019). Demands for biofuel have driven the conversion of

agricultural land to maize in North America and sugarcane in South America, creating tensions with food production, deforestation and exposing plant-derived bioenergy as not necessarily “clean” nor “green.” Bioethanol derived from maize has a high carbon footprint due to the fossil fuel-derived fertilizers required for its cultivation (Fairley, 2011; Mekonnen et al., 2018; Stehfest, Ross, & Bouwman, 2010), whereas the sugarcane industry has a lower carbon footprint because the bagasse waste product from the initial energy recovery is then used to cogenerate heat and electricity displacing energy required for bioethanol production (Mekonnen et al., 2018), even taking into consideration carbon emissions from crops burned prior to harvest (de Figueiredo, Panosso, Romão, & La Scala, 2010). Electricity generated directly from biomass from major agricultural crops is more efficient than producing biofuel, and tends to be more water efficient (Gerbens-Leenes, Hoekstra, & van der Meer, 2009). Sugar beet, maize, and sugarcane are the most favorable crops for electricity or bioethanol generation, while potato (*Solanum tuberosum*, Solanaceae) is also favorable for bioethanol in temperate environments only (Gerbens-Leenes et al., 2009). However, water required for electricity generation is influenced by the environment as well as the crop; for example, electricity generated from sugarcane in Cuba and Pakistan requires twice the water needed

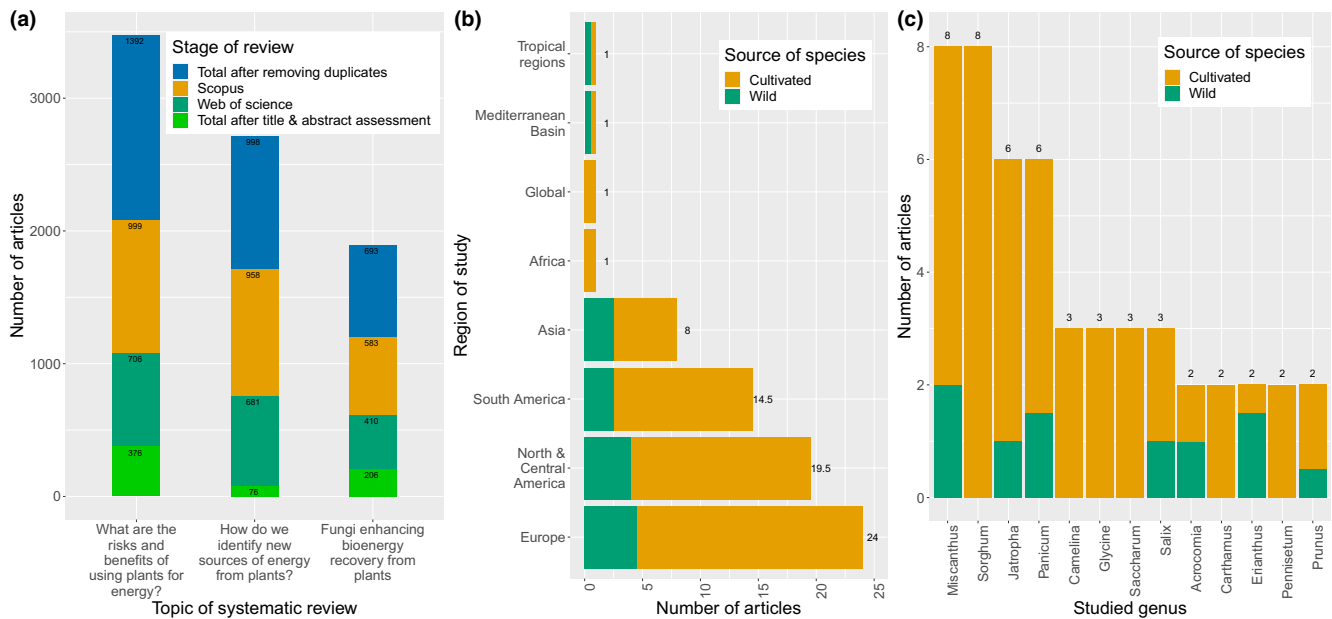


FIGURE 4 Results of systematic reviews to characterize research on the plant and fungal kingdoms as sources of bioenergy showing (a) pre- and post-filtering systematic reviews; (b) geographical; and (c) taxonomic research trends evidenced by volume of literature identified by systematic review of identification of new plant resources suitable for bioenergy (see Methods S1)

in regions of Peru, Argentina, Colombia, and Brazil (Gerbens-Leenes et al., 2009; Gerbens-Leenes & Hoekstra, 2012). Brazil is by far the largest producer of sugarcane-derived bioethanol (91% of global production from September 2016 to October 2019) (OECD & FAO, 2019) and is also the main consumer, due to its large fleet of flex-fuel vehicles that can run on either gasohol (a mix of gasoline and anhydrous ethanol) or on E100 (hydrous ethanol) (OECD & FAO, 2019).

Possible tensions between bioenergy production and water resource availability is one area in which new water-efficient feedstocks could expand the potential for developing bioenergy technologies, particularly in dryland environments. *Prosopis* (Fabaceae) trees are associated with N-fixing bacteria, and have been found to maintain higher productivity under drought and heat stress in comparison with other widely recommended species for arid lands (*Leucaena leucocephala*, *Parkinsonia aculeata*, *Prosopis tamarugo*, *Cercidium floridum*, and *Olneya tesota*) and could act as a source of biomass, wood, and food products in drylands (Felker, 1998; Felker, Cannell, Clark, & Osborn, 1983). More recently, xeric plants that use Crassulacean acid metabolism (CAM) have been considered for their potential as sustainable dryland bioenergy feedstocks. Their lower water requirements per unit of dry biomass than C_3 and C_4 crops as well as their water storage capacity help them overcome the limitation of intermittent water availability (Borland, Barrera Zambrano, Ceusters, & Shorrocks, 2011). *Agave* (Asparagaceae) and *Opuntia* (Cactaceae) species can operate at near-maximum productivity with low water requirements (Borland et al., 2011; Borland, Griffiths, Hartwell, & Smith, 2009) and exhibit lower greenhouse gas emissions and nitrogen leaching than maize (Davis et al., 2012). *Opuntia ficus-indica* and *Euphorbia tirucalli* (Euphorbiaceae) have also been considered potential bioenergy crops and been determined to produce promising

yields with low rainfall (Mason et al., 2015) but require careful consideration of the potentially negative ecological impact of introducing invasive species outside their natural range (Grace, 2019). In a global scale GIS-based productivity model, simulations for the year 2070 on low-grade land suggested that *Opuntia ficus-indica* alone has the capacity to meet extreme bioenergy scenarios ($>600\text{ EJ yr}^{-1}$) and is highly resilient. *Opuntia ficus-indica* and *Agave tequilana* (both CAM) outperformed the C_4 bioenergy crop *Panicum virgatum* in modeled arid zones (latitudinal range 30°S – 30°N) (Owen, Fahy, & Griffiths, 2016). *Agave* bioenergy production systems have been determined by life cycle analysis to provide increased energy outputs and greenhouse gas offsets compared to maize or switchgrass (Yan, Tan, Inderwildi, Smith, & King, 2011) as well as being far more water efficient (Davis, LeBauer, & Long, 2014) due to the high water content of their tissues, and relative ease with which tissue is digested (Yang, Lu, et al., 2015; Yang, Cushman, et al., 2015).

The establishment of new bioenergy feedstocks and crops is dependent on agricultural, economic, and social factors (IEA, 2019) beyond the immediate tensions with food, water, and biodiversity. Societal issues such as market access, finance, and policy frameworks determine whether new bioenergy technologies and feedstocks will become established. Market linkages, access to institutional support, and micro-finance stimulate farmers' investment and adoption of sustainable technologies policies and programs (Shiferaw, Okello, & Reddy, 2009). In rural Ethiopia, factors such as trust in government support, credit constraints, market access, and spouse education influence farmers' uptake of sustainable agricultural practices being adopted (maize–legume rotation, conservation tillage, animal manure use, improved seed, and inorganic fertilizer use) (Teklewold, Kassie, & Shiferaw, 2013). Wealthy, educated, young male farmers are most

likely to adopt new technologies in Ethiopia, as they are able to afford the risk if the technology fails (Melesse, 2018). However, barriers such as the complex bureaucratic governance structure and misalignment of policies can undermine all these interventions, as has been shown in Indonesia (Bößner et al., 2019). Governance and policy are crucial to encourage transition to bioenergy and reduce people's dependence on non-renewable energy sources, particularly as population growth increases energy needs. Many countries in sub-Saharan Africa (Mohammed, Mokhtar, Bashir, & Saidur, 2013) and India (Luthra, Kumar, Garg, & Haleem, 2015) have national renewable energy policies but not fully formed regional policies.

Afforestation in countries such as Madagascar and Ethiopia with *Grevillea* species (Proteaceae, native to Australia) for primary fuel has resulted in unexpected land transformation due to the preferences of local people for native rather than exotic species (Kull, Harimanana, Radaniela Andrianoro, & Rajoelison, 2019). Similarly, cultivation of *Jatropha curcas* L. (Euphorbiaceae), a species native to Central and South America, for seed oil has had limited success in Africa and Asia (Antwi-Bediako, Otsuki, Zoomers, & Amsalu, 2019; Castro Gonzáles, 2016). Obstacles included the lack of effective technologies for community processing (Moniruzzaman, Yaakob, Shahinuzzaman, & Khatun, 2017), strenuous and time-consuming fruit collecting (Pari, Suardi, Longo, Carnevale, & Gallucci, 2017), and skin irritation caused by handling (Devappa, Roach, Makkar, & Becker, 2013). *Jatropha curcas* can be invasive outside its native range (Prentis et al., 2009) and future climate scenarios will increase its invasive potential (Dai et al., 2018). By comparison, a sustainable seed oil industry has been successfully established in East Africa based on the indigenous tree species *Croton megalocarpus* Hutch. (Euphorbiaceae). The species is used as a biofuel for electricity (Jacobson, Shr, Dalemans, Magaju, & Ciannella, 2018). One micro-enterprise, EcoFuels Kenya (efk.co.ke), sources > 3,000 tonnes of wild-collected nuts per year through a proprietary collection network. Processing of the nuts yields seedcake which is used as animal feed and husks pressed into briquettes are sold to the coal firing industry.

With increasing awareness of the climate crisis, attention is turning to carbon capture technologies in addition to renewable energy production. To date, plants have provided large-scale solutions to reducing atmospheric carbon dioxide such as forests (Bonan, 2008; Kukrety, Wilson, D'Amato, & Becker, 2015) and grasslands with belowground biomass (Scurlock & Hall, 1998). Improving carbon storage potential is now a breeding target for perennial fast-growing bioenergy crops such as *Miscanthus*, which store carbon in long, lignified roots and do not require annual ploughing (Christensen, Lærke, Jørgensen, & Kandel, 2016; Xue, Lewandowski, & Kalinina, 2017). *Miscanthus* has even been proposed to be substituted for maize on currently available croplands in the US, potentially using half the land and one-third of the water to produce the same amount of bioethanol, which could be further improved with advanced biofuel conversion technology (Qianlai Zhuang, Qin, & Chen, 2013). There has been significant research into the role of perennial plants such as *Miscanthus* in enhancing carbon capture and storage (e.g., Agostini, Gregory, & Richter, 2015), although in the context of energy crops

this has tended to concentrate on the restricted set of species listed in Box 1 and shown in Figure 4c. This research suggests that while currently used perennial energy crops may not impact soil organic carbon levels (Ferchaud, Vitte, & Mary, 2016; Ye & Hall, 2020), they do positively impact carbon draw-down and storage within the plant, but choice of species is critical to achieve carbon capture outcomes (Di Vita, Pilato, Pecorino, Brun, & D'Amico, 2017). We propose that a diversity-driven approach to plant and fungal energy sources could also involve research to identify novel perennial taxa that simultaneously maximize carbon capture and storage while a standing crop. Plant roots appear to differentially take up carbon (Kell, 2012) and increased atmospheric CO₂ appears to disproportionately increase biomass and yield in tuberous crops such as cassava (*Manihot esculenta*, Euphorbiaceae) (Rosenthal et al., 2012) that can be used in energy production (Okudoh, Trois, Workneh, & Schmidt, 2015). Perennial plants also often offer advantages including year-round harvesting, better abiotic and biotic stress resilience, and supply of a broader range of ecosystem services when compared with shorter lived plant species (Borrell, Biswas, Goodwin, & Blomme, 2019).

3 | DISCOVERING NEW ENERGY SOURCES FROM PLANTS

New bioenergy solutions could bring considerable gains, beyond the downstream benefits of reduced energy poverty, to biodiverse nations. The Nagoya Protocol of the Convention on Biological Diversity (CBD) (United Nations, 2011) enshrines the sovereign ownership of biodiversity, and equitable sharing of benefits derived from it. The grass genus *Miscanthus* (Poaceae) is among the first crops for which bilateral agreements have been developed under the CBD to guide the breeding of new varieties from wild germplasm collections from Asia (Huang et al., 2019). In recent decades, a naturally occurring sterile triploid hybrid, *Miscanthus* × *longiberbis* (= *Miscanthus* × *giganteus*), has been grown commercially to overcome the drawback of invasiveness associated with other *Miscanthus* spp. cultivated for bioenergy. Such precedents establish high standards for the identification and development of other species for bioenergy feedstocks, particularly in regions of high biodiversity. This potential is significant, given that commonly used sources of bioenergy comprise a small fraction of the immense diversity of the plant and fungal kingdoms (Box 2). Known records are a conservative reflection of the diversity of species already used. For instance, a recent update to the useful plants of Colombia (<http://colplanta.org>) highlighted 20 additional fuel species; we would expect a similar degree of underreporting in all of the world's most biodiverse countries (Figure 4).

Selecting the right plant species is important because different technology platforms require feedstocks that vary in properties such as lignin, carbohydrate, cellulose, moisture, and lipid/oil content (Box 1). Generally, thermal conversion technologies (pyrolysis, combustion, gasification) require low moisture content feedstocks with high lignin and low ash content, whereas

biological conversion (fermentation, anaerobic digestion) requires wet feedstocks rich in carbohydrates. Among the top-level criteria for new energy plants is that they do not compete with resources needed for food production, do not contribute to non-sustainable harvesting and biodiversity loss, and reduce carbon emissions. High value co-products may increase the feasibility of certain bio-fuels. Biodiesel production generates *ca.* 10% glycerol as the main byproduct (Yang, Hanna, & Sun, 2012) that is often considered a waste product. However, crude glycerol has been investigated as a source of reduced carbon for the model diatom *Phaeodactylum tricornutum* and did not reduce photosynthetic capacity, or cell growth, suggesting crude glycerol could be used to increase biodiesel production or other co-products from *P. tricornutum* (Villanova et al., 2017). The production of microalgal biofuels could also become more feasible if produced alongside high value co-products in a biorefinery producing multiple products from microalgae such as proteins, pigments, vitamins, and antioxidants (Chew et al., 2017; Li, Liu, Cheng, Mos, & Daroch, 2015).

The search for promising new candidate species for new uses, in this case as feedstocks for bioenergy technologies, depends on specialist knowledge of plant taxonomy and accurate comparative data compiled by experts. Closely related plant species with shared morphological (phenotypic), chemical and physiological similarities are readily identified by their taxonomic (Alston, Mabry, & Turner, 1963) and phylogenetic (Rønsted et al., 2012) relationships. However, this approach has limitations when the aim is to identify candidate species that may be morphologically dissimilar to relatives known to possess a trait of interest (e.g., domesticated crops and their wild relatives), if the trait has not been systematically characterized in a plant group, and if highly novel candidate species are sought. In those cases, candidate species can be predictively identified from the clades in the tree of life in which that trait is most likely to occur (Ernst et al., 2016; Grace, 2019; Rønsted, Savolainen, Mølgaard, & Jäger, 2008; Zhu et al., 2011). Machine learning analysis, recently successful in the search of new antibiotics (Stokes et al., 2020), could help to separate the search for candidate species from their classification or tree of life altogether, facilitated by curated trait datasets (Kattge et al., 2020). Screening for properties such as oil or carbohydrate content, wood density, habitat or cultivation preferences is, however, needed to populate these comparative datasets, rendering these data capture efforts as key priorities.

A predictive approach to finding new energy sources from trait datasets is feasible using the relatively well resolved tree of life (Leebens-Mack, Barker, Carpenter, & Deyholos, 2019) and comparative trait data available (Kattge et al., 2020) for the plant kingdom. This approach is likely to be less effective for the approximately 72,500 species of algae, due to the considerable taxonomic uncertainty in their classification (Guiry, 2012). For the fungal kingdom, with <5% of species scientifically identified and named (Hawksworth & Lücking, 2017; Willis, 2018), biological screening programs, focused on ecological and environmental parameters rather than traits in known species, will be the most viable option for discovering new useful properties in the as-yet undocumented species. In the bioenergy sector, fungi are mainly

used in the pre-treatment of lignocellulosic biomass and expansion of these applications may be one of the most rewarding research areas. The identification of fungal species new to science will likely reveal yet more species suitable for bioenergy applications.

4 | FUNGI ENHANCING PLANT-BASED BIOENERGY PRODUCTION

The fungal kingdom is one of the most promising untapped natural resources for addressing global energy challenges. Fungi enhance bioenergy recovery from biomass and are able to utilize the waste products of bioenergy processes to produce yet more bioenergy, such as waste glycerol from biodiesel production (Fakankun, Mirzaei, & Levin, 2019), seafood processing plant effluent (Cheirsilp, Suwannarat, & Niyomdech, 2011), and waste coffee pulp (Menezes et al., 2013). The basidiomycete white-rot fungi are the most widely used for delignification of bioenergy feedstocks, as they completely mineralize lignin in aerobic conditions (Saritha & Arora, 2012). Recently, the addition of rumen liquid has been found to improve the efficiency of biogas production by anaerobic fungi typical of grazing animal digestive tracts (Gruninger et al., 2014; Nagler, Kozjek, Etemadi, Insam, & Podmirseg, 2019).

Fungal enzymes produced by species such as the filamentous *Trichoderma reesei* (Gupta et al., 2016) break down plant biomass and are a renewable and abundant resource for bioenergy production (Singh, Harms, & Schlosser, 2014; Vasco-Correa & Shah, 2019). Agricultural waste can be broken down by fungal cellulases into sugars and are subsequently fermented by yeast producing bioethanol (Saini, Saini, & Tewari, 2015). Microbial fuel cells can be run on fungal enzymes (such as those from *Saccharomyces cerevisiae*) to generate electricity from plant biomass (Allen & Bennetto, 1993; Mathuriya & Sharma, 2010). Fungi are usually used for their redox-active fungal proteins in the anode or in the cathode as enzymes catalyzing the reduction of a terminal electron acceptor (mainly oxygen) (Sekrecka-Belniak & Toczyłowska-Mamińska, 2018).

Lipids produced by oleaginous fungi from a plant-based substrate can be used in biofuel production. *Saccharomyces cerevisiae*, *Mortierella isabellina*, and the yeast *Cystobasidium iriomotense* (Tanimura et al., 2018) produce lipids, including from feedstock derived from plant biomass such as sweet sorghum, *Sorghum bicolor* (L.) Moench (Poaceae) (Economou, Aggelis, Pavlou, & Vayenas, 2011). The yeast *Yarrowia lipolytica*, can produce lipids from a seawater-based medium and crude glycerol (a by-product of biodiesel production) which could alleviate freshwater use for industrial purposes, such as growing media (Dobrowolski, Drzymala, Rzechonek, Mitula, & Mironczuk, 2019; Fukuda, Kondo, & Noda, 2001).

Mycorrhizal fungi act as symbionts for *ca.* 90% of vascular plants (Brundrett & Tedersoo, 2018) and may enhance bioenergy recovery. Mycorrhizal fungi can increase yields through improved nutrient and water acquisition and resistance to both

foliar and root pathogens (Allen, 2007, 2011; Campos-Soriano, García-Martínez, & Segundo, 2012; Smith, Jakobsen, & Smith, 2000; Wehner, Antunes, Powell, Caruso, & Rillig, 2011; Wehner, Antunes, Powell, Mazukatow, & Rillig, 2010). For instance, shoot phosphorus content is increased by arbuscular mycorrhizal fungi in the grass species *Brachypodium distachyon* Roem. & Schult., (Poaceae) a potential feedstock for bioenergy production (Hong et al., 2012). Re-establishing the natural level of arbuscular mycorrhizal fungi richness (which act as symbionts for ca. 72% of vascular plants (Brundrett & Tedersoo, 2018)) could even be considered a valid alternative to conventional fertilization practices (Berruti, Lumini, Balestrini, & Bianciotto, 2016). Arbuscular mycorrhizae enhance stress tolerance and production in other bioenergy crops, such as castor bean (*Ricinus communis* L.; Euphorbiaceae) (Zhang, Hu, Zhang, Tian, & Guo, 2018), switchgrass (Jach-Smith & Jackson, 2020), and sugarcane (*Saccharum spontaneum* L.) (Mirshad & Puthur, 2017). Bioenergy crop yields may also be significantly increased with the application of other fungi, such as the endophyte *Helminthosporium velutinum*, which has been determined to significantly increase biomass yields in *Sorghum bicolor* (Diene, Takahashi, Yonekura, Nitta, & Narisawa, 2010).

5 | CONCLUSIONS AND RECOMMENDATIONS

The plant and fungal kingdoms have untapped potential to address energy poverty (SDG 7) and diversify the bioenergy sector with sustainable, local sources of feedstock matched to emerging technologies. Established supply chains from North America and South America currently dominate global bioenergy production, and regions with the highest energy security and least biodiversity currently support intensive research efforts on a few well-known plant species. Opportunities abound to refocus research and development toward the most appropriate species and renewable technologies to address energy poverty and enhance global access to clean, green bioenergy. We make the following recommendations to stakeholders in the bioenergy sector to harness the potential of plants and fungi to reduce energy poverty in an environmentally sustainable way:

Researchers and funding bodies should scale efforts to identify new sources of bioenergy from native plant species in the Global South where energy poverty is most acute and plant diversity exceptionally rich (see Box 2). Efforts should focus particularly on sub-Saharan Africa and Oceania (excluding Australia and New Zealand). We emphasize the importance of screening programs with different approaches to optimize the identification of plant and fungal species new to science with potential as native feedstocks in multipurpose systems. Accurately identified reference collections in botanic gardens and seed banks, as well as fungal culture libraries and algal collections, are invaluable for accelerating these studies. Species which can be grown on degraded or marginal lands, or harvested during invasive plant clearance efforts, should be prioritized.

Industry should prioritize investment in technologies developed for native species and multi-purpose systems, which provide the full spectrum of ecosystem services in bioenergy landscapes such as foods, carbon storage, shade, water management, air quality, pollinator support, and biocultural value. Modeling using natural capital approaches should be used to select species and ecosystems. Technologies minimizing waste from bioenergy production processes, or high-yielding native plants, fungi or offshore-cultivated algae, are priorities to reduce the impact of bioenergy production on land use and terrestrial biodiversity, as explained in Section 3, above.

Governments and international aid programs should urgently prioritize the implementation of energy-efficient stoves in households, and ovens for small-scale industries, where timber and charcoal extraction is linked to high levels of biodiversity loss and poverty. Partnerships with communities, researchers, and industry, supported by governments, are needed to embed clean and green bioenergy technology, educate communities about sustainable harvesting, and provide training to manage infrastructure. Policy frameworks at the local and national level are needed to embed bioenergy technologies with financial incentives. These could include subsidies, micro-finance, crop insurance, assured markets and minimum support prices declared by government for compulsory farming of bioenergy crops such as pulses or oilseeds.

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AUTHORS' CONTRIBUTIONS

O.G., J.C.L., and P.W. designed the study; O.G., C.G., J.M., I.O., S.P., O.P., and P.W. analyzed data; all authors contributed to the manuscript and agreed to the final version.

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SUPPORTING INFORMATION

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